

NOTES ON FALL PLUMAGES, WEIGHTS, AND FAT CONDITION IN THE RUBY-THROATED HUMMINGBIRD

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BETWEEN September 6 and 24, 1955, a notable concentration of Ruby-throated Hummingbirds (*Archilochus colubris*) was observed in extensive patches of *Crotalaria spectabilis* in the Savannah River Plant area, southwestern Aiken County, South Carolina. In this seasonal or aspect community of leguminous, yellow-flowered herbage, the hummingbirds perched, hovered, drank nectar, gave squeaky callnotes, fought one another, dashed about in various directions, and otherwise made themselves conspicuous. The birds seemed to set up vague territories or defended areas, which brought to mind Pitelka's (1942:200) reference to fall concentrations of hummers in which individuals were mutually hostile and manifested belligerence to the extent that "a sort of vestigial territoriality" was seen. In the *Crotalaria* patches the birds were present not only in the daytime but also at night, as dawn and dusk observations indicated. With such an aggregation of hummingbirds close at hand it seemed almost mandatory that one avail himself of the opportunity for detailed study. Accordingly, some 30 hours were spent netting live birds, collecting others for study of plumages, weights, and fatness, and making incidental observations. In order to round out the study of fat deposition, additional specimens were collected from middle Georgia and northern Florida.

HABITAT AND POPULATION

Standing two to three feet high, the *Crotalaria* grew thickly in three major patches, each occupying about one acre. There were additional smaller patches and strips, especially along road edges. The total area dominated by the legume was estimated at roughly four acres. Most of the neighboring areas were old fields in which composites (*Heterotheca* and *Haplopappus*) and grasses (*Andropogon* and *Digitaria*) were especially prominent. A wooded strip along a stream was situated about 100 to 200 yards from the areas blanketed with *Crotalaria*. Not infrequently Rubythroats would fly to this wood, and possibly some of them roosted here. It was reckoned that between 100 and 150 hummingbirds were aggregated in the *Crotalaria* patches and their near vicinity. This suggests that there were at least 25 birds per acre, hardly an overestimate for early September. Insofar as could be told, numbers had reached a maximum or a near maximum on September 6, the time of our first visit; the population had dwindled somewhat by September 16, and had fallen off rather suddenly, to only a few individuals, by September 23. The last date on which hummers were seen here (or elsewhere in the region) was Sep-

tember 24; at this time only two or three were noted. Many of the *Crotalaria* flowers were present fully a week after the birds had departed.

During their sojourn, the Rubythroats were the only birds present in the patches, which might be called, in ecologic terms, a "*Crotalaria-Archilochus* Aspect Association." Large bees (*Bombidae* and/or *Xylocopidae*) were also conspicuous members of this relatively simple, seasonal community. Although Pitelka (1942:191) and others have described altercations between Rubythroats and bees, none was observed in the *Crotalaria* patches.

NETTING AND ATTEMPTS AT COLOR-MARKING

The first objective was that of catching with Japanese mist nets some of the hummingbirds for color-marking, with a view to elucidating the behavior of individuals and something of the nature of territoriality in this autumnal aggregation. This endeavor was successful only in the sense that the birds could be caught, weighed, sexed, and color-marked; it was unsuccessful in that no repeat records were established. Mist nets placed along swaths cut through the herbs, or where a patch stopped at the edge of a road, were moderately successful in catching fast-moving hummingbirds at various times of day. Many birds slipped through or out of nets, and some were adept at "braking" just short of nets and backing off or otherwise maneuvering away. Too, many of them flew around or, more commonly, over the nets. Occasionally, to the watcher's dismay, one would even perch on the top trammel of a net. In general the hummers were more skillful in avoiding the nets than are many passerine birds. They were not only capable of learning what to avoid but also possessed, to use terms from Bené (1945:15), "an aerial perspective . . ., an unobstructed view of the total configuration, [which] facilitates perception of spatial relations. . . ." With two to four nets set up, each 30 to 40 feet long, it was found that about one Rubythroat per hour could be ensnared and handled—a slow rate by some standards but one that might prove satisfactory to one making special studies of individuals or small populations of hummingbirds.

Each bird caught was slipped into a vial, its head protruding, and a cap of aluminum foil with a perforation just large enough to slip over the hummer's head was secured to the open end of the vial with a rubber band. A bird thus immobilized could be weighed and color-marked. Ten birds so handled (including five of either sex) were marked by means of small celluloid color bands suspended from the throat. The band was attached with thread and Duco cement to small elastic loops, and the elastic was stretched by an improvised expander and slipped over the diminutive head. On some birds an extra bit of cement was used to make the elastic adhere to certain of the neck feathers. The desired effect, as the bird might be viewed from

some yards away, was that of a bright ornament (red, blue, yellow, or a combination) bulging or hanging from the throat region. In spite of the dubious outcome of this particular marking attempt, it would seem that the above-sketches method or some modification of it might prove effective for hummingbirds with respect to seasonal or short-term marking.

SPECIMEN COLLECTIONS

Specimens for laboratory study collected with .22 caliber shot cartridges lost little blood, and they were weighed within a few minutes of the time of collection. With some specimens, nectar flowed out of the throat and mouth onto the balance pan; it was clear that nectar, perhaps more than small insects, was an important source of nutriment. Two specimens were prepared as study skins; others were preserved as flattened, dried parts (bill, tongue, throat feathers, spread wings, and rectrices). The rest of the specimens, including seven from the *Crotalaria*, four from middle Georgia, and one from the Gulf Coast of western Florida, were given to Connell for analysis of fat content.

SECONDARY SEX CHARACTERS

Size and plumage coloration.—An investigator marking and releasing Rubythroats in the postbreeding period will naturally wish to rely on external characters for recognition of males and females. As is generally known, adult male Rubythroated Hummingbirds may be identified at any season by their dark, metallic red throats and their relatively-narrow, unspotted rectrices. Since females of this species, and apparently of the entire genus *Archilochus* (Bent, 1940:358), are larger than males (cf. Ridgway, 1911:629), one could identify females vs. immature males by recording dimensions of wing, tail, bill, etc. However, such measurements are neither the most rapid nor, it would seem, the most reliable way of determining sex in this species. Nor can throat coloration be used in all instances, for although some immature males have one or more red throat feathers this is not always the case. Furthermore, while Ridgway's (*loc. cit.*) statement that the young female is "similar to the young male, but throat without dusky streaks," does indicate a tendency, it does not provide adequate means for identifying young hummers as to sex. More specifically, the short streaks or spots on the throat, grayish to dusky in the young male, are usually paler, more blurry, in the young female, but this sex difference is subtle and may almost overlap, so that the observer, unless he has studied carefully the throat markings in series of immature Rubythroats, will probably err in his judgment of some individuals.

Tail spots.—According to the series at hand, the fourth rectrix (from the outside) of females shows at least a trace of white at the tip. By contrast

young males, which otherwise display white tail-spots similar to those of females, show no trace of white on this rectrix.

The sixth primary.—In the present study the shape of the sixth primary (or the fifth counting from the outermost, or tenth, primary), a feather that seems not to have been used by previous workers, proved the most reliable single character for determining sex irrespective of age. It is true that Ridgway, in his characterization of the genus *Archilochus*, says that the "six innermost primaries [are] abruptly narrower than the rest, with the edge of [the] inner web forming a more or less prominent angle subterminally." Now among these six narrow primaries, the outermost, or sixth, is conspicuously narrower than those (the seventh through the tenth) lying distal to it; this holds not only for adult males but also for immature ones. In males the tip of this primary is more pointed and more abruptly angulated than in females. Also its outer web tapers so as to become extremely narrow along the distal half of the feather. Subterminally, the width of this outer web is approximately 1 mm. in females, whereas it is 0.3 mm. or less in males (a difference readily seen at a glance).

AGE CHARACTERS

The distinctiveness of the adult male has already been mentioned. Adult females are not so easily singled out, and they might be confused with young females in the postbreeding or premigration season. Ridgway (1911:629), although helpful, does not make a direct comparison of females of the two age classes. In our series only one adult female (taken in mid-September) was available for plumage comparison. This specimen resembled most of the young hummers in that extensive molt was apparent over head, breast, and belly regions. The old bird, but not the young, also was molting the upper tail coverts, which were mere pinfeathers. Although the Rubythroat is said to have a complete molt in spring (*vide* Bent, 1940:358), we find no mention of its molting extensively in September. As is consonant with Ridgway's implication (*loc. cit.*), the throat and belly regions of the adult were whiter than in young females, and also the adult's flanks were more grayish, lacking the decidedly buffy tinge of the immatures. The remiges, and especially the rectrices at their tips, were more worn in the older female Rubythroat, and the remiges had a rather more brownish cast than did those of immature birds.

SEX RATIOS AND AGE RATIOS

Birds trapped or taken from the *Crotalaria* population showed an even sex ratio, 16 males to 16 females. Of this series of 32, only two (a male and a female) were adults, the rest being birds of the year. From this sample, which was obtained randomly or strictly on the basis of availability, we may

say tentatively that adults made up only about 7 per cent of the aggregation. Since three or four adult males were noticed in the group, this would tend to support the estimate that this gathering comprised 100 or more individuals.

BODY WEIGHT AND WEIGHT LOSS

Body weight.—In the Savannah River Plant area, a triple-beam balance taken into the field enabled prompt weighing, inside a car, of birds netted or shot for study purposes. The times at which birds were obtained varied, so that very little bias results from daily fluctuations in weight. The data on body weight, or total weight, of Ruby-throated Hummingbirds, as well as on heart weight relative to body weight and on fat content, are summarized in Table 1 (see Figure 1, also, for total weight). In both sexes body weight tends to fluctuate until mid-September, whereupon it increases. Just as females have larger measurements than males, so they tend to weigh more, the mean values (weighted) derived from Table 1 being 3.84 grams for females and 3.51 grams for males. A comparable difference holds for samples from both earlier and later parts of the aestivo-autumnal period. Weights of males taken on September 23 and November 4 are about 36 per cent greater than those handled from September 6 to 9; similarly, those of females taken on September 23 are some 45 per cent greater than those obtained on September 6 to 9. As may be judged from weight data in the literature and from the fact that the hummingbirds taken in earlier September already were moderately fat, the per cent increase in weight from mid- or early summer to late September would seem even more drastic, probably of the order of 50 to 70 per cent.

Weight and moisture loss.—A test of weight loss after death was made for seven specimens. Taken between 7:20 and 9:35 a.m., these were weighed almost immediately after death, then kept in small aluminum-foil cones placed inside protective paper cones, and finally weighed again after periods of 3.5 to 5 hours (the day was very hot and the cones were kept in a shady place). Weight loss in the hummingbirds in this period, which averaged more than four hours, ranged from 0.26 to 1.87 per cent, averaging 1.09 per cent. Whether paper cones alone would have checked desiccation as satisfactorily as this remains to be determined. It is our feeling that metal-foil cones provide an adequate safeguard against desiccation and consequent weight loss in small birds collected in hot weather. Such a safeguard is recommended if such specimens are to be carried for several hours before they are weighed.

As to the netted birds, it was noted that considerable moisture formed inside the vials in which Rubythroats were kept for several minutes. Inserted dry, the birds would come out damp. Dr. Eugene Odum expressed interest in this fact, commenting that "birds are not supposed to sweat." One of the

TABLE 1

BODY WEIGHT, HEART RATIO, AND FAT CONTENT IN RUBY-THROATED HUMMINGBIRDS
IN LATE SUMMER AND FALL

Males								
Date ¹	Total Body Collected and Marked		Weights: Color- Marked Birds Extremes	Heart Ratio ²	No.	Fat Content: Collected Per Cent Fat of Wet Weight		Birds Per Cent Fat of Dry Weight
	No.	Mean				Gross Ratings ³	Per Cent Fat of Wet Weight	
July 15 (G)	1	3.4	—	—	1	—	15.1	45.88
Sept. 6, 7	2	3.51	3.10, 3.92	2.04	1	(3.0)	—	—
Sept. 8	5	3.41	3.05-3.85	2.05	5	(3.0)	—	—
Sept. 9	4	3.32	2.94-3.82	1.83	1	(3.0)	—	—
Sept. 12	2	3.06	2.83, 3.36	2.26	2	(2.5)	—	—
Sept. 16	2	3.56	3.32, 3.81	1.98	2	(3.5)	18.8, 28.6	47.82, 61.05
Sept. 23	1	4.99	—	1.50	1	(5.0)	44.3	75.64
Nov. 4 (F)	1	4.20	—	—	1	—	40.6	74.08
Females								
June 11 (G)	1	3.2	—	—	1	—	11.1	33.02
Aug. 2, 11 (G)	2	3.55	3.2, 3.9	2.43	1	—	14.0	45.41
Sept. 6, 7	3	3.75	3.44-3.97	—	—	—	—	—
Sept. 8	3	3.34	3.21-3.37	1.80	2	(3.0)	—	—
Sept. 9	3	3.61	3.54-3.96	1.60	2	(3.5)	—	—
Sept. 12	3	4.03	3.64-4.34	1.58	3	(3.7)	—	—
Sept. 15 (G)	1	3.5	—	—	1	—	16.3	42.35
Sept. 16	2	4.21	4.18, 4.24	1.66	2	(4.0)	28.2, 32.6	60.13, 64.72
Sept. 23	2	5.16	4.73, 5.65	1.16	2	(5.0)	41.2, 45.9	75.37, 77.89

¹ "G" in parentheses refers to specimens taken by Johnston in the Macon, Georgia, region; "F," to a specimen taken by H. L. Stoddard in 1954 in western Florida. Four specimens (female, June 11; male, Sept. 8; female, Sept. 15; female, Sept. 16) were adults; the others were immatures.

² Heart weight expressed as a percentage of body weight, as determined for 12 males and 11 females.

³ Crude estimates, thus—1 = slightly fat, 2 = somewhat fat, 3 = moderately fat, 4 = very fat, and 5 = extremely fat; these estimates were made before the fat content was determined.

writers (Norris), having seen that nectar was an important food item, wondered whether some or most of the moisture was excreted via the cloaca and anus. It might be added that when the living hummingbirds were handled, the surrounding temperatures were usually warm to very hot. In this observation of moisture loss by closely confined hummers we might have the germ of an interesting physiological problem.

HEART RATIO

Hearts from a number of specimens were excised for weighing. First, stumps of vessels were trimmed off, blood was washed from the auricles, and

the surfaces of the hearts were gently blotted. Weights were recorded to the nearest five-thousandths gram on the same balance as used for body weights. It is apparent in Table 1 that the "heart ratio," or heart weight/body weight ratio, decreases as total body weight increases. Thus the high ratio characteristic of relatively lean Rubythroats, which seems to be 2 per cent or more even in females (cf. Hartman, 1954:468; also the August 11 specimen, Table 1), becomes increasingly obscured as the birds wax heavier and fatter with the passage of September. As Odum and Perkinson (1951:219, 229) point out for a passerine species, the heart's fat deposits, unlike those of other parts of the body, show little seasonal variation. Hence, a decrease in the heart-ratio value with increased general fat deposition, which is especially well illustrated by the data on female hummingbirds (Table 1), was actually to be expected. For this reason very fat birds are not useful in ascertaining heart ratios for comparative purposes.

Actual heart weights, in grams, were as follows: 12 males, $.071 \pm .0012$ (.065-.080); 11 females, $.063 \pm .0016$ (.055-.075). Coefficients of variability were 5.6 for males, 8.3 for females. This difference, in which the male has the larger heart, is statistically significant ($t = 4.1$; $P < .01$); it could be accentuated if expressed in terms of heart ratios for birds with little or no fat. Even the ratios for the more or less fat specimens (Table 1), while of limited value for interspecific or higher-category comparisons, provide good indications of sex differences in heart size. Thus, while the heart ratio of the fattest male was reduced to 1.50 per cent, those of the two fattest females, collected at the same time as the male, were both reduced to approximately 1.16 per cent.

FAT CONTENT OF SPECIMENS

In making fat extractions of certain of the specimens, Connell based his procedure on that outlined by Odum and Perkinson (1951:217, 218). As is evident in Table 1, both the gross estimates or ratings of fatness and the exact percentage values for extracted fat show increases in mid- and late September. Clearly the total-weight increases are due largely to increased deposits of fat. Although quite limited, the data from adult hummingbirds suggest that there are no appreciable differences in fatness with reference to age class. Immatures, which made up over 90 per cent of the aggregation in the *Crotalaria* patches, were among the fattest and heaviest of the collected birds, and they probably are typical of the species as a whole. Incidentally, the young female weighing 5.65 grams, of which 45.9 per cent was fat, is very likely the heaviest and fattest Rubythroat on record! As may be calculated from figures in the column on wet weights, the last hummingbirds shot, on September 23 and November 4, were carrying from 1.7 to 2.6 grams of fat

(averaging about 2.1 grams), a considerably heavier load than was estimated by Pearson (1950:151). As has been pointed out by Odum and Connell (1956), if Pearson's data, including figures on flight speed and rate of energy expenditure, are employed, 2.1 grams of fat should enable Ruby-throated Hummingbirds to fly about 800 miles—hence across the Gulf of Mexico.

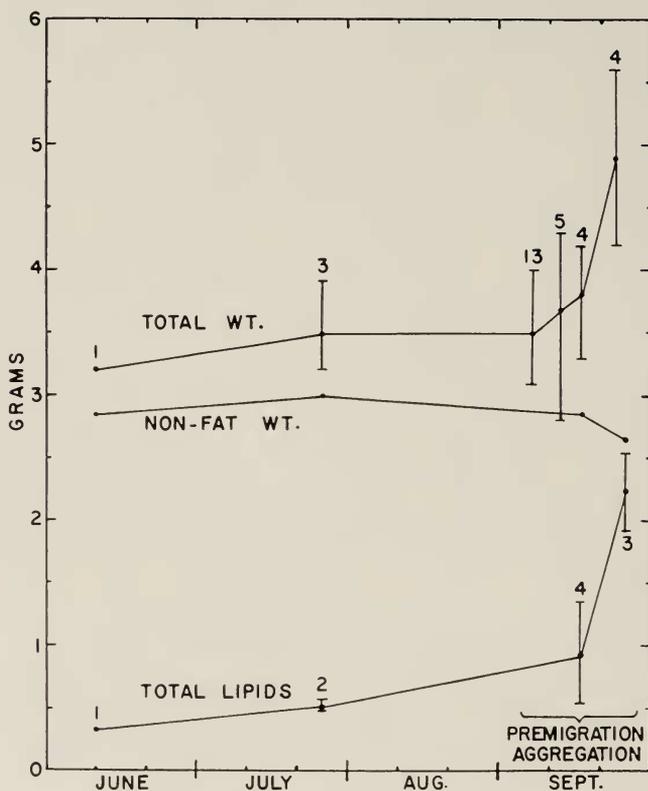


FIG. 1. Changes in weight and fat deposition in Ruby-throated Hummingbirds in late summer and fall. Numerals above vertical bars indicate number of specimens for each sample.

SUMMARY

In early September, 1955, an estimated 100 to 150 Ruby-throated Hummingbirds foraged, waged battle, and roosted in about four acres of *Crotalaria* in the Savannah River Plant area, Aiken County, South Carolina. Much of their food was nectar taken from the *Crotalaria* flowers. The birds' numbers declined after mid-September, and the last individuals were seen on Sep-

tember 24. Ten hummingbirds caught in mist nets were color-marked, but there were no repeat records. Both the shape of the sixth primary and the throat coloration provided criteria for distinguishing in the hand males and females among immatures. An adult female lacked the ventral buffiness characteristic of young females. The sexes were present in about the same numbers, but adults (male and female) seemed to comprise only about 7 per cent of the aggregation. Body weights for summer- and (especially) fall-collected hummingbirds (including some from Georgia and Florida) averaged about 3.8 grams for females and about 3.5 grams for males. Weights increased markedly after mid-September, as did fat content. Heart ratios, in contrast, decreased with increase in body weight and fatness; heart weight *per se* was relatively constant and was significantly greater in males than in females. Fat content, expressed as per cent of wet weight, ranged from about 11 to 15 per cent in June to about 41 to 46 per cent in heavy, premigratory individuals. The heaviest birds, each carrying about two grams of fat, were thought to have sufficient fuel to travel nonstop some 800 miles.

LITERATURE CITED

- BENÉ, F.
1945 The role of learning in the feeding behavior of black-chinned hummingbirds. *Condor*, 47:3-22.
- BENT, A. C.
1940 Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. *U.S. Nat. Mus. Bull.* 176.
- HARTMAN, F. A.
1954 Cardiac and pectoral muscles of trochilids. *Auk*, 71:467-469.
- ODUM, E. P., AND C. E. CONNELL
1956 Lipid levels in migrating birds. *Science*, 123 (3203):892-894.
- ODUM, E. P., AND J. D. PERKINSON, JR.
1951 Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory white-throated sparrows. *Physiol. Zoöl.*, 24:216-230.
- PEARSON, O. P.
1950 The metabolism of hummingbirds. *Condor*, 52:145-152.
- PITELKA, F. A.
1942 Territoriality and related problems in North American hummingbirds. *Condor*, 44:189-204.
- RIDGWAY, R.
1911 The birds of North and Middle America. *Bull. U.S. Nat. Mus.*, 50: Part V.
- 1918 HAHN AVENUE, AIKEN, SOUTH CAROLINA; DEPARTMENT OF BIOLOGY, UNIVERSITY OF GEORGIA, ATHENS, GEORGIA; AND DEPARTMENT OF BIOLOGY, MERCER UNIVERSITY, MACON, GEORGIA, JUNE 13, 1956